

*GOGODIPTERUS PADDYENSIS* (MILES), GEN. NOV.,  
A NEW CHIRODIPTERID LUNGFISH FROM THE LATE DEVONIAN  
GOGO FORMATION, WESTERN AUSTRALIA.

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ABSTRACT

A new genus of chirodipterid lungfish, *Gogodipterus* gen. nov., is erected for *Chirodipterus paddyensis* Miles, 1977, after further preparation of the holotype revealed that the palate has an unusual parasphenoid with a raised buccal lozenge that participated in the reduction of food. Other major differences between *Gogodipterus* and *Chirodipterus* are in the dentition and features of the braincase. A revised classification of the chirodipterid group is proposed in which the families Chirodipteridae Campbell and Barwick, 1990, and Stomiahykidae Bernacsek, 1977 are placed within the superfamily Chirodipteroidea superfam. nov. The family Chirodipteridae contains two subfamilies: the Chirodipterinae subfam. nov. and the Pillararhynchinae subfam. nov. *Gogodipterus* is regarded as a sister genus to *Chirodipterus* based on synapomorphies of the palate, dentition and scales, and absence of more specialized characters seen in *Pillararhynchus* and *Sorbitorhynchus*.

KEYWORDS: Devonian, Gogo Formation, Western Australia, Dipnoi, *Gogodipterus* gen. nov., Chirodipteroidea superfam. nov., Chirodipterinae subfam. nov., Pillararhynchinae, subfam. nov.

INTRODUCTION

The genus *Chirodipterus* Gross, 1933, includes two species known only from holotype material, *C. wildungensis* Gross from the Late Devonian of Germany, and *C. ouawayensis* Schultze, 1982, from the Middle Devonian of the USA, and two species from the Late Devonian Gogo Formation of Western Australia, *C. australis* Miles, 1977, and *C. paddyensis* Miles, 1977. *Chirodipterus paddyensis* was described from two specimens, a partial body and skull (the holotype) and a single right ramus of a lower jaw; because the holotype was embedded in resin the palate and lower jaw dentition was not revealed. Smith and Campbell (1987) further described the histology and mode of growth of chirodipterid toothplates and figured the isolated lower jaw of *C. paddyensis*.

The holotype (Western Australian Museum (WAM) 70.4.250) has been further prepared with acid to remove all matrix from the palate and braincase, and the resin slab cut in order to separate the lower jaw from the skull, revealing for the first time the nature of the palate, upper

jaw dentition and posteroventral face of the braincase (Fig. 1) as well as the lower jaw and parts of the visceral skeleton (Fig. 2). In this paper the specimen is redescribed and comparisons made with other chirodipterids. A revised classification of chirodipterids is proposed based on the phylogenetic conclusions of Campbell and Barwick (1990) and this paper.

Terminology for cranial bones follows Forster-Cooper (1937). Institutional prefixes to catalogue numbers: BMNH, British Museum (Natural History), London; WAM, Western Australian Museum, Perth.

SYSTEMATIC PALAEONTOLOGY

**Superfamily Chirodipteroidea nov.**

**Diagnosis.** Dipnoans with dental tuberosities arranged radially or subradially; discontinuous basal pulp cavities; hypermineralized dentine in tuberosities and flat parts of plates; buceohypophysial foramen absent; bone A in contact with bone B, but bone A still carries

occipital commissure; pineal foramen absent; anterior furrow on mandible not confined laterally by dentary; jaw suspension moved forwards, quadrate inclined.

**Remarks.** The diagnosis is taken from characters listed in Campbell and Barwick (1990) to define the monophyly of the chirodipterid group. As their family Chirodipteridae refers only to an advanced set of taxa on their cladogram (*Chirodipterus*, *Palaedaphus*, *Sorbitorhynchus* and *Pillarrhynchus*), and excludes the Stomiahykidae, it is necessary to place the two families into a new superfamily, Chirodipteroida.

**Referred genera.** *Chirodipterus* Gross, *Pillarrhynchus* Campbell and Barwick, *Sorbitorhynchus* Wang *et al.*, *Gogodipterus* gen. nov., *Palaedaphus* Traquair, *Stomiahykus* Bernacsek, *Archaeonectes* Meyer.

#### Family Stomiahykidae Bernacsek, 1977

**Diagnosis.** Chirodipteroid lungfishes having elongated pterygoid dental plates with pointed anterior tuberosities, most of which remain isolated, arranged in rows; large tusk-like tuberosity at anterior end of mesial row.

**Remarks.** Bernacsek (1977) did not provide a diagnosis of the family, as it was monotypic as proposed, based on the characters of the genus *Stomiahykus*. The above synapomorphies are from Campbell and Barwick (1990:162).

**Referred genera.** *Stomiahykus*, *Archaeonectes*.

#### Family Chirodipteridae Campbell and Barwick, 1990

**Diagnosis.** Chirodipteroid lungfishes having pterygoid dental plates approximately as wide as long, and with an obtuse or rounded anterior end; tuberosities closely spaced or fused along the radial rows; large areas of plate without tuberosities; sutures present between parasphenoid and pterygoids; dermopalatines and anterior median plate not fused to pterygoids; adsymphyseal plate free; spiracular recess absent; cleithrum with buried concave external face; scales not rhombic and lacking articulatory pegs.

**Remarks.** The above characters are listed in Campbell and Barwick (1990:162) for defining the clade containing higher chirodipterids. Other features used to define chirodipterids (Long 1988) include the cheek with long 10 bone which contacts bones 5-7 (seen only in *Chirodipterus*

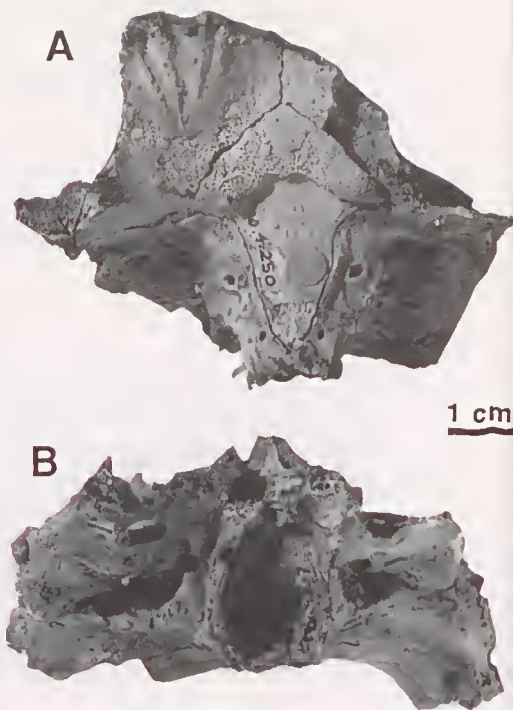


Fig. 1. *Gogodipterus paddyensis* (Miles) gen. nov., holotype WAM 70.4.250. A, palate and braincase in ventral view. B, braincase in posterior view.

and *Pillarrhynchus*), and the ploughshare-shaped parasphenoid. As this last feature is only seen in *Chirodipterus* it must now be regarded as an autapomorphy of that genus.

**Referred genera.** *Chirodipterus*, *Pillarrhynchus*, *Sorbitorhynchus*, *Gogodipterus*, *Palaedaphus*.

#### Subfamily Pillarrhynchinae nov.

**Diagnosis.** Chirodipterid lungfishes having a lower jaw with long median symphysis, and only two or three infradentaries; supra-Meckelian vacuity almost closed; preglenoid process long and high; glenoid fossa restricts lateral movement of jaw.

**Remarks.** The above characters are from Campbell and Barwick (1990: 162), with the additional character of the long median symphysis (48-56% of lower jaw length for the two genera). Other derived features of the new genera *Pillarrhynchus* and *Sorbitorhynchus* will no doubt be included to expand this diagnosis after they have been formally described.

**Referred genera.** *Pillarrhynchus*, *Sorbitorhynchus*.

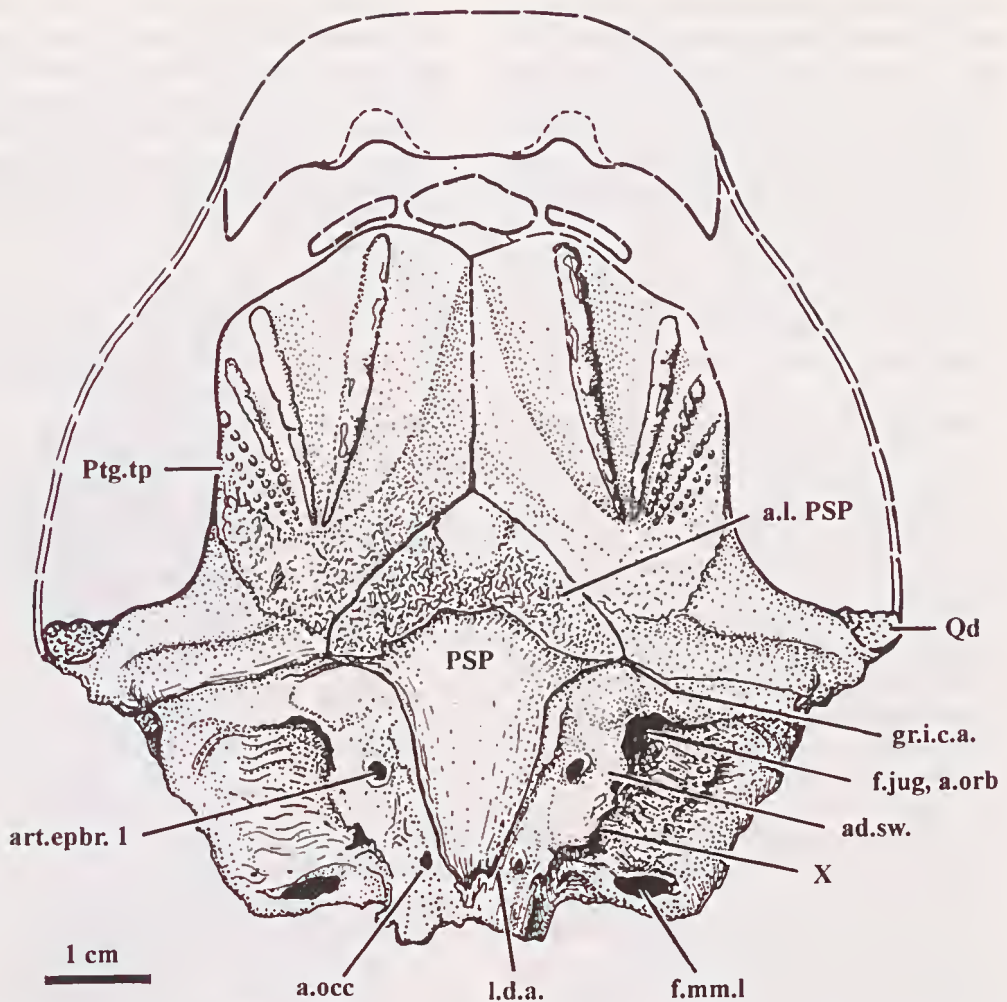


Fig. 2. *Gogodipterus paddyensis* (Miles) gen. nov., reconstruction of the palate and braincase in ventral view, based on the holotype, WAM 70.4.250.

#### Subfamily Chirodipterinae nov.

**Diagnosis.** Chirodipterid lungfishes that retain a large supra-Meckelian vacuity and have a median symphysis on the lower jaw of about 40-43% of total jaw length.

**Remarks.** The presence of the large supra-Meckelian vacuity and the smaller median jaw symphysis are not regarded as derived features within the clade, but serve only to distinguish the genera *Chirodipterus* and *Gogodipterus* from the Pillararhynchines.

#### *Gogodipterus* gen. nov.

**Type species.** *Gogodipterus paddyensis* Miles, 1977.

**Diagnosis.** Chirodipterine lungfish having parasphenoid with an anterior division with raised anteriorly pointing V-shaped ridge bearing enamel-covered dentine confluent with medial crushing surfaces of the pterygoid toothplates; dentition consists of three well-spaced high ridges which cross from labial to lingual surface and converge on the posteromesial angle, and up to three smaller outer rows of individual, non-coalescent tuberosities; small process on dorso-lateral edge of prearticular which projects over the supra-Meckelian fossa of mandible at base of the toothplate; shorter region on posterior face of braincase dorsal to foramen magnum, transverse processes lateral to foramen magnum are large.

**Remarks.** The new genus is readily distinguished from all other chirodipterids because of

the shape of the parasphenoid and the extensive, dentine-covered ledge along its anterior margins. The dentition is also unique amongst chirodipterids, all others having rows of cusps which may coalesce to form low tooth-ridges, as distinct from the sharp, high tooth-ridges separated by deep furrows seen in *Gogodipterus* gen. nov. Other characters listed by Miles (1977:12) for separating the species from *Chirodipterus australis* are now included as generic features due to the discovery of a second new species of *Chirodipterus*, from south of Lloyd Hill at Gogo, currently being studied by the author.

***Gogodipterus paddyensis* (Miles, 1977)**  
(Figs 1,2, 3A, 4A, 5, 6, 7C)

*Chirodipterus paddyensis* Miles, 1977, pp.1, 3, 12-13, 38, 45-46, 66, 69, 83, 96, 113, 115-116, 132, 153, 167, 182, 200, 204-207, 231, 236-7, 247-248, 253, 255, 259, 273-274, 276-279, 293; Figs. 3a,b; 19-2, 38, 85, 107, 121 b-h, 145-146, 148.

*Chirodipterus paddyensis* - Smith, 1977, p.53

*Chirodipterus paddyensis* - Schultze, 1982, p.161.

*Chirodipterus paddyensis* - Marshall, 1987, p.19

*Chirodipterus paddyensis* - Smith and Campbell, 1987, p.333, 339, 342-343; Pl.3, Figs 14-17, Fig.32.

*Chirodipterus paddyensis* - Long, 1987, p.310.

*Chirodipterus paddyensis* - Long, 1988, p. 440.

*Chirodipterus paddyensis* - Long, 1991, p. 395.

*Chirodipterus paddyensis* - McNamara, Long and Brimmell, 1991, p. 88, 89 Fig.3.

**Description.** Miles (1977) has described and figured much of the anatomy of *Gogodipterus paddyensis*, including the posterior and lateral surfaces of the braincase, the lower jaw (based on BMNH P56034), the subopercular and opercular bones, and parts of the visceral skeleton. The following new features are described herein: the parasphenoid (ventral surface), pterygoid toothplates, hyomandibular and new observations on the lower jaw (based on holotype) and the ceratohyal are included. Comparisons are made directly with other chirodipterids, based on the descriptions of *Chirodipterus wildungensis* (Gross 1933; Säve-Söderbergh 1952; Jarvik 1967), *C. australis* (Miles 1977, Campbell and Barwick, 1982a, 1982b, and several specimens in the Western Australian Museum), *Stomialhykus* (Bernassek 1977; Smith and Campbell 1987); *Pilliarhyuchus* (Campbell and Barwick 1990), *Archaeopectes* (Meyer 1859), *Palaedaphus* (Traquair 1878) and *Suuwaptia* (Thomson 1967).

*The braincase.* Miles (1977) gave a detailed description of the dorsal, posterior and postero-lateral regions of the braincase, as these were the only exposed surfaces on the holotype. The specimen now also shows the ventral surface of the braincase posterior to the pterygoid toothplates. In general, the braincase of *Gogodipterus* (Fig. 3A) is not as deep as that of *Chirodipterus australis* (Fig. 3B) or *Pilliarhyuchus* (Fig. 3C). The ventral surface of the braincase exposed posterior to the quadrates is proportionally broader (Breadth/Length index = 250) than for *Chirodipterus australis* ( $B/L_i = 225$ ) or *C. wildungensis* (c.195).

Most of the anatomical features of the ventral surface correspond well to those described for *Chirodipterus australis*, except for the development of the foramina interpreted by Miles as for the lateral division of the masseter muscle (f.mm.1, Fig. 3B). In modern lungfish (e.g. *Neoceratodus*) the masseter muscles pass posterodorsally from the lower jaw, in front of the quadrate to insert on the rear dorsal region of the braincase, not onto the posterior face of the braincase. It seems more likely that these foramina are for venous drainage of the braincase. In *Chirodipterus australis* this foramen is clearly shown in ventral view, and in posterior view is barely visible. In *Gogodipterus* this foramen has more of a posteroventral orientation, and is only partially seen in ventral view, being more clearly shown in posterior view (Fig. 3A).

The articulation for the first epibranchial is large on *Gogodipterus* (art.epbr 1, Fig. 2) relative to that in *Chirodipterus australis*, and the adotic swelling (ad.sw, Fig. 2) has a small lateral groove developed in *Gogodipterus* which is absent in *Chirodipterus*. The foramen for the jugular vein (f.jug, Fig. 2) is preceded by a well-defined entrance groove in *Gogodipterus*, but not in *Chirodipterus*.

In posterior view, the area of hypaxial trunk muscle attachment dorsal to the foramen magnum and ventral to the fossa for the temporalis muscle is proportionately much shorter in height on *Gogodipterus* than for *Chirodipterus* or *Pilliarhyuchus* (Fig. 3). There is no occipital crest present in *Gogodipterus* (Miles 1977: Fig. 19) as is developed in *Chirodipterus australis* (ero, Fig. 3B). The transverse processes (tr.pr, Fig. 3A) developed lateral to the foramen magnum are larger and more distinct in *Gogodipterus* than in *Chirodipterus australis* (Fig. 3B).

The features of the lateral surface of the braincase of *Gogodipterus* is very similar to

those of other *Chirodipterus* species as far as is known. However, on the diagram of Miles (1977: Fig. 21) the foramen labelled as the optic nerve (II) is here interpreted as being the foramen for the ophthalmic artery (Fig. 4A, a.om). This is because on all other chirodipterids where the brinease is preserved (*Chirodipterus australis*, *C. wildungensis*, *Stomiahykus*, Fig. 4C-D) the

first foramen anterior to the profundus canal (V1) and foramen jugulare is always the ophthalmic artery. The position of the optic nerve foramen in *Gogodipterus* would be slightly anterodorsal to the ophthalmic artery foramen, and this area is not preserved on the specimen.

In addition to these differences in brinease anatomy, Miles (1977:45-46) notes the following differences between *Gogodipterus paddyensis* and *Chirodipterus australis*: the lateral occipital fissure is closed immediately behind the foramen jugulare, but is open more dorsally, and extends upwards well into the midline; the foramen jugulare shows weakly defined subdivision into nervous and venous openings, as distinct from *Chirodipterus australis* in which the two openings are well-defined.

*The parasphenoid.* The parasphenoid of *Gogodipterus* (PSP, Fig. 2) measures 39.6mm long by 29 mm wide. The anterior division, as exposed ventrally, measures 16mm in length, being approximately 40% of the bone's length (in *Chirodipterus australis* this is 36%, in WAM 86.9.692). The anterior edge of the bone is formed into a raised platform that forms an inverted V-shape, and this ledge (a.l.PSP, Fig. 2) rises approximately 3.3 mm high from the level of the midline of the ventral surface of the bone. This raised ledge is covered by 'vermiform dentine' made up of enamel-covered denticles (Smith and Campbell 1987: 343) which is covered in the middle of the ledge by small blebs of smooth enamel-covered dentine, confluent with the level of the mesial edges of the pterygoid toothplates.

It is clear that the raised ledge of the parasphenoid was actively used in crushing food, greatly enlarging the crushing surface of the palate beyond the area of the toothplates. This utilisation of the parasphenoid in feeding is otherwise only seen in few dipnoans: the chirodipterid *Pillararhynchus longi* (Campbell and Barwick 1990), the chirodipterid *Stomiahykus* (Campbell and Smith 1987, fig.18) and the Permian *Conchopoma* (Schultze 1975). In addition to these, a new species of *Chirodipterus* being studied from the Gogo fauna by the author also has small blebs of dentine on the parasphenoid, but in its dentition and overall morphology it closely resembles *Chirodipterus australis*. The damaged areas of the brinease on the holotype of *Gogodipterus paddyensis* reveal that the anterior end of the parasphenoid is not plough-share shaped as in *Chirodipterus australis*

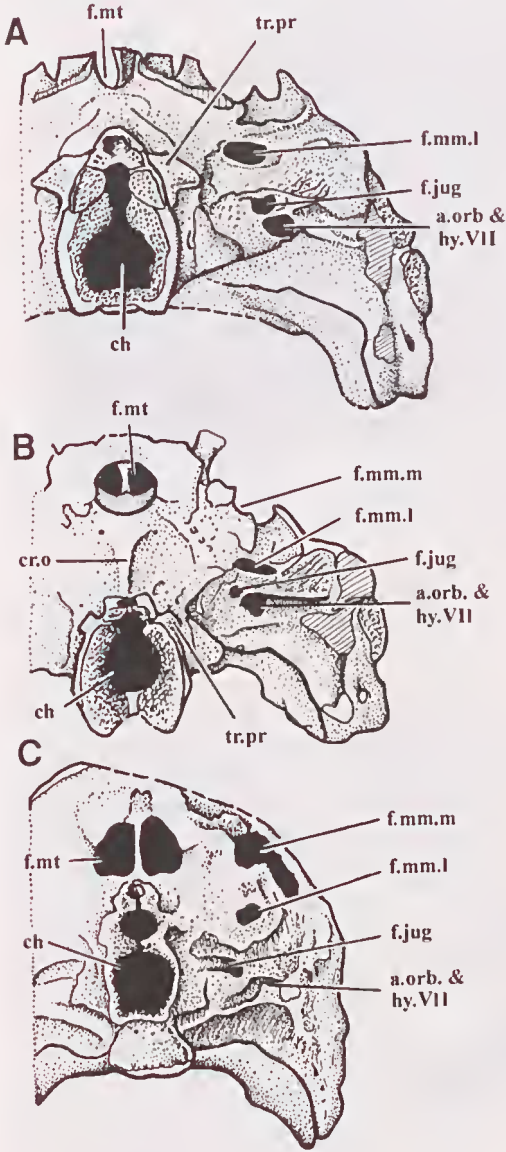


Fig. 3. Chirodipterid brineases in posterior view. A, *Gogodipterus paddyensis* (Miles) gen. nov., holotype WAM 70.4.250. B, *Chirodipterus australis* (after Miles, 1977: Fig. 16). C, *Pillararhynchus longi* (after WAM 86.9.695).

(Campbell and Barwick 1982a: Fig. 6). The thickness of the parasphenoid at its anterior extent is 4.7mm.

*Pterygoid toothplates.* Much of the right pterygoid toothplate is preserved (Figs 1A, 2, Ptg.tp), lacking only the anterior margin. It shows three well-developed tooth ridges, the mesial row is inclined anteromesially at an angle of  $5^\circ$  from the midline; the second and third tooth rows are directed anterolaterally, the second forming an angle of  $13^\circ$ , and the third, or outermost row,

forms and angle of  $31^\circ$  with the midline axis. Three small rows of isolated cusps form tooth-rows 4 - 6. The first tooth row shows wear of individual cusps down to a smooth ridge, yet cusp boundaries are still clearly defined. The second and third tooththrows show less wear of individual cusps, and it is clear from tooth-row 3, which is completely preserved, that about 11-13 cusps are present. The pterygoid toothplate is covered in smooth shiny dentine mesial to the tooth-rows, and with vermiform enamel-cov-

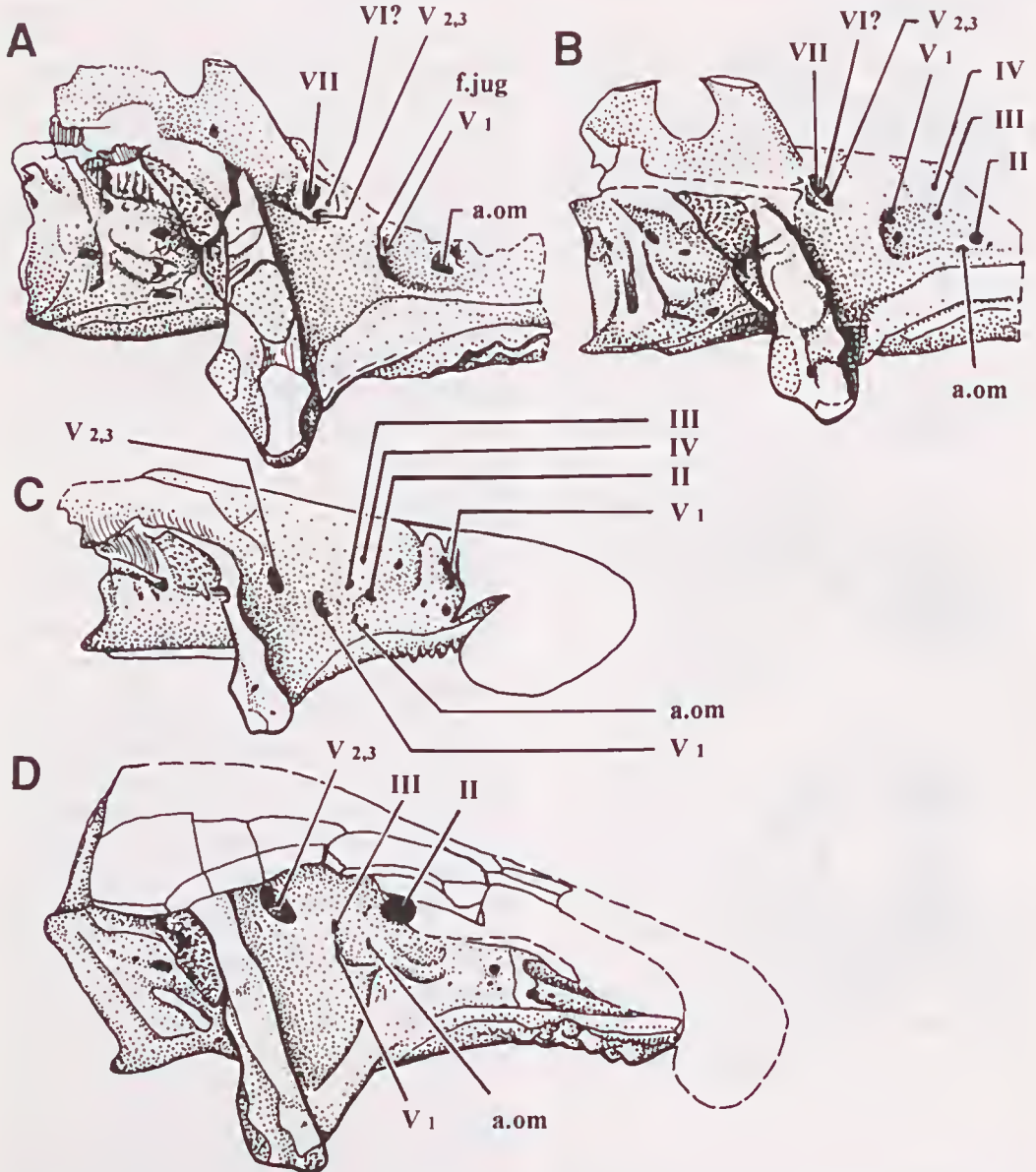


Fig. 4. Chirodipteroid brainses in right lateral view. A, *Gogodipterus paddyensis* (Miles) gen. nov., holotype WAM 70.4.250. B, *Chirodipterus australis* (after Miles, 1977, fig. 35). C, *Chirodipterus wildungensis* (after Säve-Söderbergh 1952: Fig. 5, sagittal section of skull). D, *Stomiahykus thlaodus* (after Bernacsek, 1977: Fig. 9).

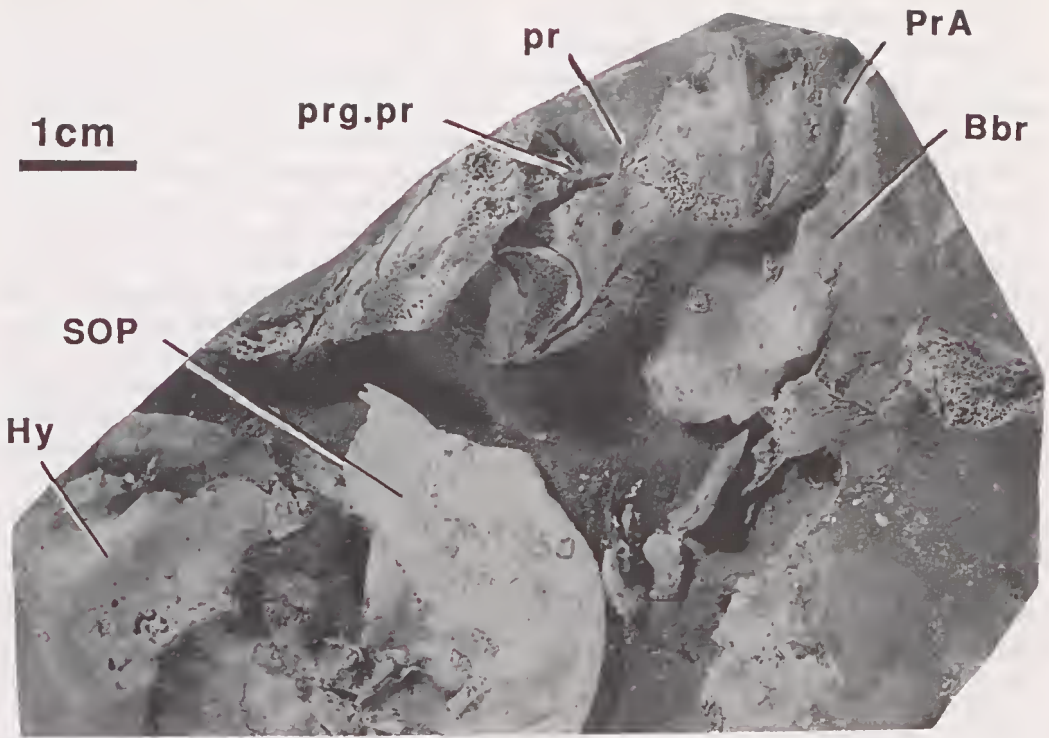


Fig. 5. *Gogodipterus paddyensis* (Miles) gen. nov., holotype WAM 70.4.250, lower jaw (left ramus), hyomandibular, subopercular and basibranchial, as prepared in situ in resin slab.

ered denticles posterior to the tooth-rows. This vermiform dentine coalesces with similar tissue on the anterior ledge of the parasphenoid.

The dentition of *Gogodipterus* differs markedly from that of *Chirodipterus australis* (as noted by Miles 1977: 293; Campbell and Smith 1987: 339), although Campbell and Smith also comment that "the plate type and structure and mode of formation of the tuberosities leave no doubt that the two species are closely related". This holds true for many of the chirodipterid group and no doubt also applies to the genus *Pilliararhynchus*, whose toothplates more closely resemble those of *Chirodipterus australis* in their wear patterns and general shape than those of *Gogodipterus*.

**Hyomandibular.** Miles (1977:273) described the hyomandibular of this species, but was unsure whether the truncus hyomandibularis VII nerve passed through a foramen in the bone (as in *Chirodipterus australis* and *Griphognathus*) or passed through a notch on the anterior margin. The new preparation has shown both sides of the hyomandibular well-preserved (e.g. Fig. 5, Hy) indicating that it bore a strong notch for the

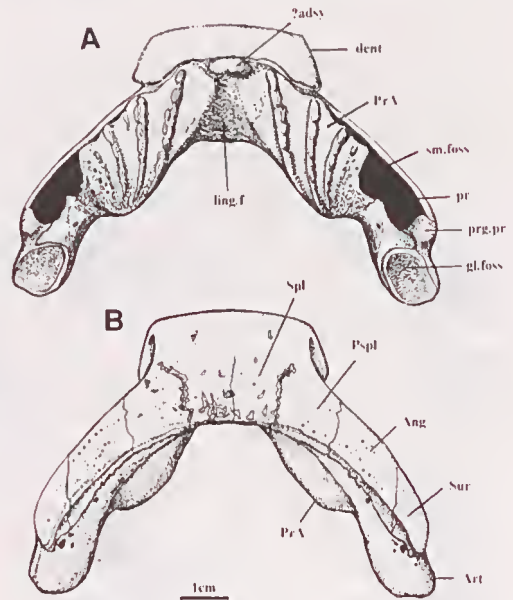


Fig. 6. *Gogodipterus paddyensis* (Miles) gen. nov., reconstruction of mandible in dorsal (A) and ventral (B) views, based on holotype WAM 70.4.250 and isolated lower jaw ramus P. 56034 (from Miles, 1977: Fig. 107).

passage of the nerve. In all other respects it is similar to that of *Chirodipterus australis*.

**Ceratohyal.** As described and figured by Miles (1977: Fig. 145), the ceratohyal of this species closely resembles that of *Chirodipterus australis* except for the fact that it is more robust and is said to lack a lateral endochondral attachment area. Miles (1977:275) suggested that the equivalent area on the lateral crest of the ceratohyal has coarse depressions and ridges which probably served the same function. Although the figure of the ceratohyal in Miles (1977: Fig. 145) shows the right element, his description is actually based on the left bone, as the right ceratohyal was only recently prepared, and it is poorly preserved. The lateral crest of the left ceratohyal shows that it bears a well-defined groove along its equivalent to the groove above the lateral crest on the ceratohyal of *Chirodipterus australis* (Miles 1977: Fig. 142). The ceratohyal of *Gogodipterus* is also slightly more elongated, having a height to length index of 39 compared to that of c. 43 in *C. australis*.

**Basibranchial.** Two of the basibranchial bones are preserved in the holotype, situated mesial to the left lower jaw ramus. The anterior basibranchial (B.br, Fig. 5) is missing the anterior third of its length, but when reconstructed

appears to be of similar shape and proportions to that of *Chirodipterus australis* (Miles 1977: Fig. 147e). A small bone can be seen lying ventral to the anterior basibranchial, it is approximately 13 mm in length, and is probably the posterior basibranchial. It is not as highly arched anteriorly as that of *C. australis* (Miles 1977: Fig. 149), being about one third as high as it is long. In all other respects it is similar to that of *C. australis*.

**Lower jaw.** The nearly complete right ramus of this species was described by Miles, based on P56034 (Miles 1977: Fig. 107), and a further description of the dentition of this specimen was given by Smith and Campbell (1987). The left lower jaw ramus of the holotype shows clearly the posterior end of the jaw, enabling a restoration of the entire lower jaw to be accurately made by combining features of P 56034 with those of the holotype (Fig. 6), and matching these to the lower jaw tooth-ridges of the palate. The most notable features are the great width of the mandible and its well-developed lingual furrow (ling.f, Fig. 6A). The supra-Meckelian fossa (sm. foss, Fig. 6A) is invaded by a short process (pr) emerging from the prearticular (PrA), which presumably divided the jaw muscles into the anterior suborbital fibers and the larger adductor

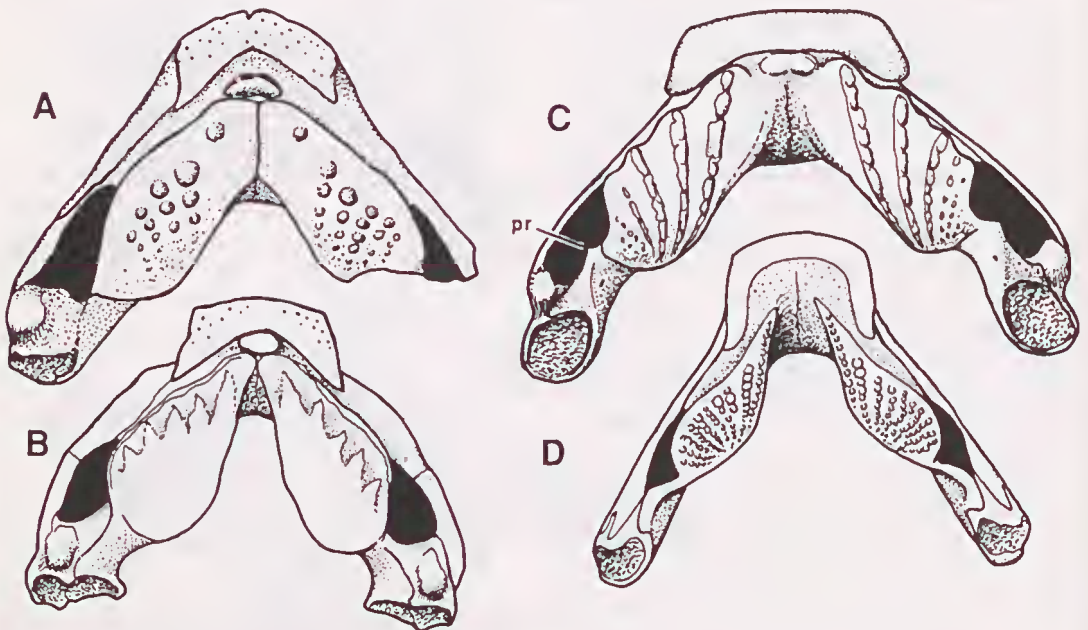


Fig. 7. Dipnoan lower jaws in dorsal view, A-C, chirodipterids, D, dipterid. A, *Chirodipterus wildungensis* (after Jarvik, 1967). B, *Chirodipterus australis*, WAM 86.9.692. C, *Gogodipterus paddyensis*, reconstructed from holotype, WAM 70.4.250. D, *Dipterus valenciennesi* (after Jarvik, 1967).



mandibulae fibers (Lauder 1980). In dorsal view the glenoid fossa (gl.foss) is well-exposed, having a more dorsally facing orientation than for other chirodipterids. It does not restrict the lateral movement of the jaw as occurs in *Sorbitorhynchus* and *Pillararhynchus* (Campbell and Barwick 1990). The preglenoid process (prg.pr) is well-developed as in other chirodipterids, but is not as high as in pillararhynchines (Campbell and Barwick 1990). The dentary (dent) is a very broad bone as shown in the reconstruction, and matches well the overall broad proportions of the palate and skull.

**Etymology.** After the Gogo Formation (named after Gogo Station) of the Canning Basin, Western Australia, and the well known Devonian lungfish genus *Dipterus*.

#### RELATIONSHIPS OF *GOGODIPTERUS* GEN. NOV.

The chirodipterid group was considered to be monophyletic by Long (1988:445) who suggested that *Pillararhynchus* ("new chirodipterid", WAM 86.9.695) was a primitive sister taxon to *Chirodipterus* plus *Stomialyktus*, based on the

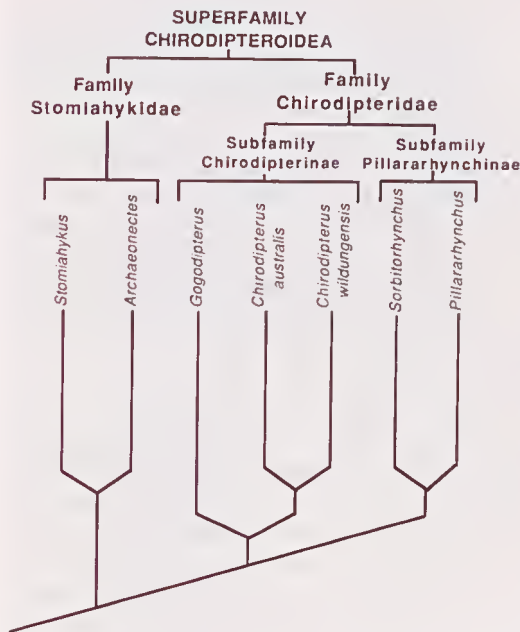


Fig. 8. Interrelationships and classification of chirodipteroids, based on characters discussed in the text (synapomorphies given in diagnoses of higher taxonomic groups).

shared feature of the notochordal pit being separated from the foramen magnum. There was a misprint in this work which should have said that the condition was opposite to what was stated, as in *Chirodipterus* the foramen magnum has merged with the notochordal pit. However, on the evidence of primitive dipnorhynchids having a similar condition to that of *Chirodipterus* and *Stomialyktus* (Campbell and Barwick 1982a: Figs 1-3), I now see the condition in *Pillararhynchus*, where the foramen magnum is separated from the notochordal fossa, as a specialised condition, probably related to the fact that *Pillararhynchus* has an extremely deep braincase.

A more detailed list of synapomorphies defining the chirodipterid group was given recently by Campbell and Barwick (1990). Their phylogenetic results are embodied in the classification presented in the front of this paper. Campbell and Barwick erected the new family Chirodipteridae, based on the synapomorphies given in the diagnosis in this paper. Both *Chirodipterus* and *Gogodipterus* are more advanced phylogenetically than the stomialyktids in a number of characters, such as closed pinal foramen, jaw suspension moved more anteriorly etc. (listed in Campbell and Barwick 1990:162).

These two genera are regarded as more plesiomorphic than *Pillararhynchus* and *Sorbitorhynchus* in lacking the synapomorphies of the pillararhynchines (e.g. almost closed supra-Meckelian vacuity, very large preglenoid process). It is not clear at present whether *Gogodipterus* and *Chirodipterus* share any synapomorphies that might define them as a monophyletic group (Chirodipterinae), or are sister taxa to each other plus the Pillararhynchinae. For convenience they have been placed in the new subfamily Chirodipterinae because of similar shared vascular and nervous foramina pattern seen on the lateral surface of the braincase in the orbital region. Figure 4 shows that the exit foramina for the profundus nerve (V1) is situated higher on the lateral wall than the optic foramen (II) in *Chirodipterus* species (Fig. 4B, C) and presumably in *Gogodipterus* (Fig. 4A), than for *Stomialyktus* (Fig. 4D). Another feature that might unite the *Chirodipterus* species with *Gogodipterus* is the shape of the foramen for the lateral division of the masseter muscle (Fig. 3, f.mm), which is slit-like in these forms but more rounded, and smaller in overall size, on *Pillararhynchus* (Fig. 3C).

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